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Faria, Larissa; Alexander, Mhairi E.; Vitule, Jean R.S.

Published in:
Fisheries Management and Ecology

DOI:
[10.1111/fme.12353](https://doi.org/10.1111/fme.12353)

Published: 16/11/2019

Document Version
Peer reviewed version

[Link to publication on the UWS Academic Portal](#)

Citation for published version (APA):

Faria, L., Alexander, M. E., & Vitule, J. R. S. (2019). Assessing the impacts of the introduced channel catfish *Ictalurus punctatus* using the comparative functional response approach. *Fisheries Management and Ecology*, 26(6), 570-577. <https://doi.org/10.1111/fme.12353>

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1 **Assessing the impacts of the introduced channel catfish *Ictalurus punctatus* using**
2 **the Comparative Functional Response approach**

3 **Abstract**

4 In the metric “Relative Impact Potential” (RIP), the functional response (FR) of a non-
5 native species can be compared to that of a native analogue and combined with the species
6 abundance to predict its environmental impact. Here, using the River Guaraguaçu (Brazil)
7 as a case study, this methodology was implemented to identify the impacts of the non-
8 native channel catfish *Ictalurus punctatus* compared to a native species *Rhamdia quelen*
9 towards small prey fish. Both species exhibited Type II FRs, however handling times
10 were lower for *I. punctatus*, resulting in a greater maximum feeding rate in this species.
11 Consequently, an $RIP > 1$ was found, indicating that *I. punctatus* represents a superior
12 impact to prey when compared to its native analogue. These results demonstrate that *I.*
13 *punctatus* is a potential threat to small endangered fish species. Therefore, policies to
14 avoid escapes from aquaculture should be created and the abundance of *I. punctatus*
15 controlled.

16 **Keywords**

17 alien species, aquaculture, fish, freshwater, management, Relative Impact Potential

18

19 **1 Introduction**

20 The introduction of non-native species to novel regions is one of the main drivers of
21 species extinction and is considered the second major cause of global biodiversity loss
22 after habitat destruction (Bellard, Cassey & Blackburn, 2016; Clavero & García-Berthou,
23 2005; Vitousek, D’Antonio, Loope & Westbrooks, 1996). Predation by non-native
24 species can devastate native prey populations as non-native predators are often more
25 efficient consumers of resources compared to their native counterparts (Paolucci,
26 MacIsaac & Ricciardi, 2013; Salo, Korpimäki, Banks, Nordström & Dickman, 2007;
27 Simberloff & Vitule, 2014). Compounding this, native prey often do not exhibit effective
28 anti-predator behaviour due to a lack of shared evolutionary history with the new predator
29 (Cox & Lima, 2006). These mechanisms can explain the establishment success of non-
30 native predators and their negative impact in the recipient community (Gallardo, Clavero,
31 Sánchez & Vilà, 2016; Latini & Petreere, 2004; Sharpe, De León, González & Torchin,
32 2017; Simberloff et al., 2013; Trumpickas, Mandrak & Ricciardi, 2011).

33 Prediction and quantification of impacts of non-native species is of great
34 importance for conservation of biodiversity, although there is no agreed standard
35 methodology for doing so (Kumschick et al., 2015; Parker et al., 1999; Ricciardi, Hoopes,
36 Marchetti & Lockwood, 2013). The comparative functional response (CFR) has been
37 proposed as an approach that “can unify invasion ecology” (Dick et al., 2017a), providing
38 a trait-based methodology for measuring resource-use interactions of non-native species
39 as a means of predicting their potential ecological impact. The CFR approach is based on
40 the comparison of the functional response (FR) of non-native and trophically analogous
41 native species, where the difference in the magnitude of the FR can predict and quantify
42 the relative impacts of the non-native species (Dick et al., 2014).

43 A FR is defined as the relationship between consumption rate and resource
44 density (Holling, 1959b). There are three types of FR: Type I – an increasing linear
45 relationship between resource density and consumption until a threshold of satiation;
46 Type II – a decelerating rate of consumption that reaches an asymptote at higher densities;
47 and Type III – an S-shaped curve where the consumption rate first accelerates at low
48 densities and then decelerates towards satiation (Holling, 1959b). The FR type of the
49 predator can have direct effects on the stability of the prey population, for instance Type
50 II FR has destabilising effects with high consumption at low densities, whereas Type III
51 has stabilising effects with a refuge of predation at low densities (Oaten & Murdoch,
52 1975; Sinclair et al., 1998). As FRs measure the *per capita* effect of a non-native species,
53 it can be combined with the abundance of the species in the field, in a metric called the
54 Relative Impact Potential (RIP), to enhance the predictive power of this approach (Dick
55 et al., 2017b).

56 A native to North America, the channel catfish (*Ictalurus punctatus* Rafinesque,
57 1818) has been introduced worldwide for aquaculture and sport fishing purposes (CABI,
58 2019). The species was first introduced in Brazil in 1971 and, having potentially escaped
59 accidentally from aquaculture cages (Orsi & Agostinho, 1999; Welcomme, 1988), it is
60 now widely found in Brazilian water bodies (Cruz-Spindler et al., 2012; Ota, Message,
61 Graça & Pavanelli, 2015; Zanatta et al., 2010). As a non-native species, *I. punctatus* is a
62 potential threat to local fish assemblages through competition and predation of native
63 species (e.g. Matsuzaki et al., 2011; Townsend & Winterbourn, 1992; Troca & Vieira,
64 2012). For example, the decline and extinction of species, such as the razorback sucker
65 *Xyrauchen texanus*, in communities invaded by *I. punctatus* has been reported (CABI,
66 2019). Additionally, *I. punctatus* demonstrates high rates of dispersal, which is aided by
67 its ability to adapt to a wide range of habitats (Olden & Poff, 2005).

68 The aim of the present study was to apply the CFR approach and the RIP metric
69 to assess the potential impacts of the invasive *I. punctatus* in a highly-diverse river in
70 Brazil, the River Guaraguaçu. The abundance of the species is not constantly monitored,
71 but there are reports about the establishment of this species in the river basin, as well as,
72 in other basins of the Paraná State (Vitule, Umbria & Aranha, 2005; Vitule, 2008). Based
73 on the species traits and invasion history of *I. punctatus* (Gutierre, Vitule, Freire &
74 Prodocimo, 2014; Tatarenkov, Barreto, Winkelman & Avise, 2006; Townsend &
75 Winterbourn, 1992; Wellborn, 1988), and considering its taxonomic distinctiveness
76 within the recipient community (Ricciardi & Atkinson, 2004), the likely impact of *I.*
77 *punctatus* on native species and ecosystems is through an elevated consumption of small
78 stream fishes.

79 To address the paucity of research on non-native species impacts in South
80 American countries (Bellard & Jeschke, 2016; Speziale, Lambertucci, Carrete & Tella,
81 2012; Vitule, Freire, Vazquez, Nuñez & Simberloff, 2012), the present study aims to
82 enhance the understanding of the impacts of introduced predators in the Neotropical
83 region, where biodiversity is both rich and threatened (Lowry et al., 2013; Myers,
84 Mittermeier, Mittermeier, da Fonseca & Kent, 2000).

85 **2 Methods**

86 2.1 *Species used*

87 *Ictalurus punctatus* is a nocturnal forager that uses a variety of habitats with preference
88 for shallow warm waters (Bailey & Harrison, 1948; Braun & Phelps, 2016; Jordan,
89 Neumann & Schultz, 2004), detecting food using olfactory and visual cues (Becker,
90 1983). Young *I. punctatus* feed mainly on insects, but adults are usually omnivorous and
91 prey also on fish (Bailey & Harrison, 1948; Braun & Phelps, 2016; Hill, Duffy &

92 Thompson, 1995; Tyus & Nikirk, 1990). The species has opportunistic behaviour and is
93 generalist, preying on a wide range of available resources in non-native regions (Endo et
94 al., 2015; Haubrock et al., 2018).

95 The FRs of the non-native channel catfish *I. punctatus* were compared to a native
96 consumer, the South American silver catfish *Rhamdia quelen* (Quoy & Gaimard, 1824),
97 which is a benthic species widely distributed in lakes, reservoirs and rivers of Central and
98 South America (Gomes, Golombieski, Gomes & Baldisserotto, 2000; Silfvergrip, 1996).
99 There are few studies on the biology of *R. quelen*, which like *I. punctatus* is representative
100 of the Siluriformes and is generally described as nocturnal and omnivorous when mature
101 (Bailey & Harrison, 1948; Gomes et al., 2000; Goudie, Davis & Simco, 1983). Adults
102 of *R. quelen* are considered generalists, feeding on fish, crustaceans, insects, vegetation
103 and organic detritus (Guedes, 1980; Meurer & Zaniboni Filho, 1997). *Ictalurus punctatus*
104 and *R. quelen* have many similarities in their anatomic digestive systems and diet
105 (Piedras, Pouey & Moraes, 2006) which make *R. quelen* an appropriate resident
106 comparator for *I. punctatus* in the FR experiments described here.

107 Both species also spawn in the spring, with temperature an important factor in
108 reproduction (Becker, 1983; Gomes et al., 2000). *Rhamdia quelen* has low fecundity rates
109 and do not present parental care (Gomes et al., 2000). Females of *I. punctatus* have around
110 8,000 eggs per kg body weight and males guard the eggs during a period of incubation of
111 5 to 10 days (Becker, 1983). *Ictalurus punctatus* reaches sexual maturity at 300–375 mm
112 in total length (TL), whereas *R. quelen* generally matures at 134–175 mm TL (Gomes et
113 al., 2000; Jackson, 2004; Shephard & Jackson, 2005).

114 Blue tetra *Mimagoniates microlepis* (Steindachner, 1877), a congeneric of the
115 locally and nationally threatened *M. lateralis* (Abilhoa & Duboc, 2004; Rosa & Lima,
116 2008; MMA, 2014), is abundant in natural water bodies and was used as prey in

117 experimental trials. Both *Mimagoniates* species are sympatric and are representatives of
118 Glandulocaudinae, which is characterised by small stream fishes (Braga, Braga, & Vitule,
119 2013; Menezes & Weitzman, 2009). *Mimagoniates lateralis* is the smallest species of the
120 genus, reaching maximum 40 mm standard length (Menezes & Weitzman, 2009; Rosa &
121 Lima, 2008).

122 2.2 *Experimental design*

123 For the experimental protocol (Figure S1), which was approved by the Ethics
124 Commission on the Use of Animals of the Biological Sciences Department of the Federal
125 University of Paraná (CEUA/BIO UFPR – Certificate n°1027), juveniles of predator fish
126 species (*I. punctatus* and *R. quelen*) were obtained in local aquaculture farms and stored
127 in tanks of 300 L in the lab. Each species was kept in a different tank with constant
128 aeration and filtration for acclimation during 30 days. Prey fish were collected in the field
129 using fishing nets and kept in an 80 L aquarium, with constant aeration and filtration, and
130 were also acclimated for 30 days. The temperature in the lab was kept at 22–26°C under
131 a natural light regime. During the acclimation period predators were fed every 48 h with
132 sausage to standardise prior experience.

133 Experiments were performed in 10 L opaque plastic boxes (35 × 20 × 25 cm)
134 with constant aeration. Individuals of predator species were randomly selected one day
135 prior to use and placed in the experimental aquariums for 24 h acclimation. Predators (n
136 = 9 per species) were size-matched with respect to total length (*R. quelen*: 16.39 cm ±
137 1.15 and *I. punctatus*: 16.83 cm ± 2.14; Students' t -test, $t = -0.55$, $df = 16$, $p = 0.59$). Each
138 predator specimen was reused in two more trials with different initial densities. After the
139 acclimation period, they were held without food for 72 h to standardise hunger levels.
140 Predators were then presented with the prey at five initial densities (2, 5, 10, 20, and 30
141 individuals), with five replicates per density. Prey were also size matched with respect to

142 total length by visual selection (≈ 3 cm). Experiments were initiated at 14:00 and prey
 143 consumption was recorded after 24 h. Controls were three replicates of each initial density
 144 of prey in the absence of predators.

145 2.3 Data analysis

146 The FR type was determined from a logistic regression of prey density by the proportion
 147 of consumed prey, as proposed by Juliano (2001). A negative first order term indicates a
 148 Type II FR, whereas a positive first order term followed by a negative second order term
 149 indicates a Type III FR (Pritchard, Paterson, Bovy & Barrios-O'Neill, 2017). The FR
 150 curves and the parameters attack rate (a) and handling time (h) were modelled using
 151 Maximum Likelihood Estimation (Bolker, 2008) with the Rogers' (1972) random
 152 predator equation that considers the depletion of prey without replacement along the
 153 experimental period:

$$154 \quad N_e = N_0 \{1 - \exp [a (N_e h - T)]\} \quad (1)$$

155 where N_e is the number of prey consumed, N_0 is the initial density of prey, a is the attack
 156 rate, h is the handling time and T is the experimental period, given in days. The attack
 157 rate (a) is the instantaneous capture rate, *i.e.* the rate at which the consumer encounters
 158 resource items per unit of resource density; and the handling time (h) is the time spent
 159 capturing and consuming the prey item (Brose, 2010; Holling, 1959a; Jeschke, Kopp &
 160 Tollrian, 2002). The h was used to estimate the maximum feeding rate ($1/hT$), which
 161 represents the FR curve asymptote. To compare the FR of each species, the parameters a
 162 and h were compared between predators using the indicator variables method, as the
 163 following equation:

$$164 \quad 0 = N_0 - N_0 \exp \{[a + Da(j)] \{h + Dh(j)\} (N_e) - T\} - N_e \quad (2)$$

165 where j is an indicator variable that takes value 0 for *R. quelen* and 1 for *I. punctatus*. The
166 parameters D_a and D_h estimate the differences between the predators in the value of the
167 parameters a and h , respectively. If these parameters are significantly different from zero,
168 then the two species differ significantly in the corresponding parameters (Juliano, 2001).
169 To visualise the uncertainty around the fitted functional responses, 95% confidence
170 intervals were constructed by bootstrapping ($n = 2000$) data around FR curves. If
171 confidence intervals do not overlap, then it can be stated that species FRs differ (Paterson
172 et al., 2015). Analyses were carried in R v. 3.4.1 (R Core Team, 2015) using the ‘frair’
173 package (Pritchard et al., 2017) at 0.05 significance.

174 The Relative Impact Potential (RIP) metric was calculated using the following
175 equation, according to proposed by Dick et al., 2017b:

$$176 \quad \text{RIP} = \frac{\text{FR non-native}}{\text{FR native}} \times \frac{\text{AB non-native}}{\text{AB native}} \quad (3)$$

177 where FR is the estimated maximum feeding rate ($1/hT$) and AB is the field
178 abundance/biomass of the species. When $\text{RIP} < 1$, the non-native species is predicted to
179 have less impact than the native equivalent; when $\text{RIP} = 1$, there is no impact above that
180 driven by native equivalents; whereas $\text{RIP} > 1$ indicates a likely non-native ecological
181 impact (Dick et al., 2017b). Data of total abundance and biomass were taken from
182 literature, from samples collected in River Guaraguaçu using a variety of fishing gears
183 (Vitule, 2008) (Table S1). As data from different methods of capture and of different
184 fishing efforts were compiled (Table S1), the capture per unit effort (CPUE) was
185 calculated to standardise these differences. This was the number of fishes captured
186 divided by the number of fish hooks or area of gill nets, multiplied by fishing effort in
187 hours.

188 3 Results

189 None of the prey fish died in any of the control replicates, therefore prey mortality in the
190 experimental trials was attributed to predation. Both species obtained a negative first-
191 order term from logistic regressions, indicating a Type II FR (Table 1, Figure 1).
192 Parameter estimates of the FR model were all statistically significant (Table 1). The attack
193 rate did not differ between species ($Da = -0.646$, $z = -0.447$, $p = 0.655$), but the handling
194 time was significantly lower for *I. punctatus* ($Dh = 0.053$, $z = 2.209$, $p < 0.05$), and thus
195 a higher maximum feeding rate was obtained (Table 1).

196 The RIP calculated using field data on total abundance did not demonstrate a
197 greater impact of the non-native species ($RIP < 1$, Table 2). Considering biomass, the
198 impact of *I. punctatus* was found to be similar to the native species *R. quelen* ($RIP \approx 1$,
199 Table 2). However, using CPUE data, *I. punctatus* was found to have a greater impact
200 ($RIP > 1$, Table 2).

201 4 Discussion

202 Both predator species in the present study demonstrated a Type II FR when exposed to
203 *M. microlepis*. Most, if not all, of the prey were consumed at low densities, which
204 suggests that in open waters this could lead to destabilising effects on the local population
205 (Holling, 1959a; Murdoch & Oaten, 1975; Sinclair et al., 1998). A Type II FR may
206 therefore pose a greater concern in open waters, where endangered, such as *M. lateralis*,
207 are often found to exist in small populations (IUCN, 2012; Sinclair et al., 1998).

208 The CFR approach provided evidence that *I. punctatus* is likely to exert an
209 ecological impact to native small fish prey, and it is possible that other small-bodied
210 endangered fish species suffer predation pressure from *I. punctatus* in a similar manner
211 as *M. microlepis*. Despite the overlap of FR curves of *I. punctatus* and its native
212 comparator *R. quelen* (Figure 1), the results of the present study suggest that *I. punctatus*

213 exerts a greater predation pressure on *M. microlepis*, with a significant lower handling
214 time, and therefore a higher maximum feeding rate. Lower h and consequently higher
215 $1/hT$, due to faster rates in processing prey, can explain the superior impact of invaders
216 (Alexander, Dick, Weyl, Robinson & Richardson, 2014). The lower handling time of *I.*
217 *punctatus* (Table 1) may be due to differences in the resource acquisition ability of the
218 species (Alexander et al., 2014). *Ictalurus punctatus* has taste buds across its body and
219 within its barbels, which aid in perception of food and trigger feeding behaviour (Caprio
220 et al., 1993; Valentincic & Caprio, 1994). *Ictalurus punctatus* also has relatively larger
221 eyes than other siluriform catfishes, which may facilitate visual predation in clean waters,
222 such as of the experimental conditions (Davis, 1959). The similar FRs of *I. punctatus* and
223 *R. quelen* towards the prey (Figure 1) also suggest that these species may have niche
224 overlap, resulting in either resource competition or repartition in open waters. Both
225 species seems to use the same strategy to find resources, as their barbels are sensitive to
226 amino acids or hydrolysed proteins, which triggers feeding behaviour (Caprio, 1975;
227 Broggi, 2014).

228 *Ictalurus punctatus* are less abundant than native *R. quelen* in the River
229 Guaraguaçu, which suggests a lower relative predation impact than the native species.
230 However, using standardised CPUE data, a different result emerged, with *I. punctatus*
231 presenting a higher abundance (Table 2), and therefore a potentially greater impact than
232 *R. quelen*. Using only the FR provides a modestly-powered predictor of non-native
233 species impacts, because a low FR can be compensated by high abundance in the field
234 (Lavery et al., 2017). The results obtained here, of a greater RIP using CPUE field data
235 (Table 2), are sufficient to justify the need of management and control of *I. punctatus*
236 population. Early interventions may be successful in avoiding non-native species impacts

237 (Simberloff, 2003), and in the present case, the results provide evidence to motivate the
238 immediate action to manage *I. punctatus* at low population levels.

239 Propagule pressure is widely believed to play a fundamental role on the
240 successful establishment and permanency of non-native species, contributing to its
241 continuous impact (Copp, Templeton & Gozlan, 2007; Kolar & Lodge, 2001; Ruesink,
242 2005). The juvenile *I. punctatus* used in these experiments were obtained from local
243 aquaculture, which is recognised as the major pathway of introduction of *I. punctatus* and
244 other freshwater invasive species (CABI, 2019; Casal, 2006; Gozlan, 2008; Naylor,
245 Williams & Strong, 2001). *Ictalurus punctatus* is among the most cultured freshwater
246 fishes globally, and its global total production in 2016 reached 432,932 tons (FAO, 2018).
247 There are many fish-farms in Paraná State that cultivate and sell young-of-the-year *I.*
248 *punctatus* despite a legislation that classifies this species as Category I, which has its
249 “*transportation, breeding, release or translocation, cultivation, propagation,*
250 *commercialization, donation or intentional acquisition prohibited by any means*”
251 (Environmental Institute of Paraná, 2015). Despite this, the production of *I. punctatus*
252 continues to increase, and the risk of escapes from aquaculture ponds is a constant threat
253 in Neotropical streams, contributing to a high propagule pressure (Forneck, Dutra,
254 Zacarkim & Cunico, 2016; Lima Junior, Pelicice, Vitule & Agostinho, 2012; Vitule,
255 Freire & Simberloff, 2009). This failed attempt to ban the introduction of *I. punctatus* in
256 Paraná could be responsible for the declines in status of many endemic fishes (Lima
257 Junior et al., 2018; Pelicice et al., 2017; Vitule et al., 2009). Therefore, the cultivation of
258 the *I. punctatus* should be avoided in Paraná in order to reduce its spreading into natural
259 water bodies.

260 Besides constant introductions of *I. punctatus*, the species’ reproductive
261 behaviour (guarders, nest spawners) is more specialised than that of *R. quelen*

262 (nonguarders, open substratum spawners) (see Balon, 1975). The male *I. punctatus*
263 guards the eggs until they hatch, a feature that may favour the establishment of the non-
264 native species in the field (Marchetti, Moyle & Levine, 2004; Tatarenkov et al., 2006).
265 Also, predation of *I. punctatus* by native fishes in the study region is unlikely due to the
266 dorsal and pectoral spines of *I. punctatus* (Bosher, Newton & Fine, 2006).

267 In the present study, juveniles of similar body size were used, which contrasts
268 natural populations. Predator body-size influences most aspects of feeding behaviour and
269 there are allometric relationships between body size and the FR parameters, with
270 increases in a and decreases in h as predator size increases (Brose, 2010; González-Suárez
271 et al., 2011; Miller, Crowder, Rice & Binkowski, 1992; Vucic-Pestic, Rall, Kalinkat &
272 Brose, 2010). In the case of the two study species, *I. punctatus* can reach larger adult sizes
273 than *R. quelen*, as the first can be mature at size 300 mm TL and *R. quelen* is already
274 mature at 175 mm TL (Gomes et al., 2000; Jackson, 2004; Shephard & Jackson, 2005),
275 which may lead to an increased *per capita* effect of the non-native species that could
276 influence the FR results.

277 As with many fishes, the degree of piscivory tends to increase in *I. punctatus*
278 with increasing body length (Starostka & Nelson, 1964). As juveniles were used here, it
279 can be expected a greater *per capita* effect of adults of in the field. Furthermore,
280 omnivores like *I. punctatus* tend to present a Type II FR when exposed to a single type
281 of prey, and the presence of an alternative food source may therefore affect our results
282 (Médoc, Thuillier & Spataro, 2017; Murdoch & Oaten, 1975). Indeed, alternative food
283 availability has been shown to change FRs of amphipods, killer shrimp *Dikerogammarus*
284 *villosus* and the freshwater shrimp *Gammarus pulex*, with the superior consumption of
285 the invasive *D. villosus* disappearing when it was presented with an alternative non-
286 animal food (Médoc, Thuillier & Spataro, 2017).

287 Differences in predator biomass also likely strengthen the impact of *I. punctatus*.
288 The mean biomass of *I. punctatus* specimens captured in the River Guaraguaçu was more
289 than twice of the native species and the RIP using biomass was ≈ 1 (Table 2), which
290 suggests that the impact of *I. punctatus* in the wild is greater than the native predator
291 despite its lower abundance. Neither predator species nor size alone can predict
292 consistently the FR type and its associated parameters, so both predator identity and size
293 should be considered to assess fully the potential ecological impacts of a non-native
294 species on invaded communities (Anderson, Linares, Dodson & Semlitsch, 2016; Guo,
295 Sheath, Amat Trigo & Britton, 2016).

296 It is important to consider other factors that may alter FR results, such as habitat
297 complexity (Alexander, Dick, O'Connor, Haddaway & Farnsworth, 2012; Barrios-
298 O'Neill, Dick, Emmerson, Ricciardi & Macisaac, 2015), which in some cases can change
299 the FR type and parameters. This can occur if habitat complexity acts as a refuge for prey
300 in low density (Alexander, Kaiser, Weyl & Dick, 2015) or contributes to predation of
301 ambush predators, resulting in a higher consumption rate (Santos, García-Berthou,
302 Hayashi & Santos, 2013). This context-dependency factor may also be an important
303 feature to be tested in the FR of *I. punctatus*, as the River Guaraguaçu has been invaded
304 by the African signalgrass *Urochloa arrecta*, a macrophyte that increases habitat
305 complexity (Michelan, Thomaz, Mormul & Carvalho, 2010; Thomaz & Cunha, 2010;
306 Vitule, Umbria & Aranha, 2006).

307 To quantify and predict the impacts of non-native species is of fundamental
308 importance to conservation efforts, because such data are needed in order to create plans
309 for management and control of damaging species. The CFR approach and the RIP metric
310 have been shown as an effective tool for predicting the impact of existing and emerging
311 high impact non-native species and can be performed elsewhere in a very simple fashion

312 (Alexander et al., 2014; Dick et al., 2017a, 2017b; Laverty et al., 2017). Therefore, the
313 CFR approach is of particular usefulness in both developing and developed countries
314 because data on non-native fish impacts are lacking for most species. Whereas, data on
315 non-native species impacts are even more scarce in less developed regions, where the
316 number of potentially threatened endemic species is often high (Frehse, Braga, Nocera &
317 Vitule, 2016; Lövei, Lewinsohn & Network, 2012; Nuñez & Pauchard, 2010; Vitule et
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625 **Figure legend**

626 **Figure 1.** Type II Functional Response curves for channel catfish *Ictalurus punctatus* (dashed line) and
 627 South American silver catfish *Rhamdia quelen* (solid line) preying on blue tetra *Mimagoniates*
 628 *microlepis*. Points indicate mean consumption per density. Shading represents bootstrapped ($n = 2000$)
 629 95% confidence intervals for each species.

630

631

632 **Assessing the impacts of the channel catfish *Ictalurus punctatus* using the**
 633 **Comparative Functional Response approach**

634 **Table S1.** Field data on total abundance (n), capture per unit effort
 635 (CPUE) and total biomass (in grams) of channel catfish *Ictalurus*
 636 *punctatus* and South American silver catfish *Rhamdia quelen*
 637 captured in 17 standardised samples, between 2005 and 2007, using
 638 different fishing gears. Data from Vitule (2008). Long lines were of
 639 10 m length, and gill nets were of 30×1.70 m, with exposure times
 640 in all cases being 1500 hours.

Fishing gear (and mesh size)	Effort	n	CPUE	Biomass (g)
---------------------------------	--------	-----	------	----------------

<i>Ictalurus punctatus</i>					
Longline	3 longlines with 10 fish hooks	8	0.000178		9312
Gill net (20 mm)	Gill net	5	6.54E-05		1069
Gill net (40 mm)	Gill net	4	5.23E-05		2075
Gill net (60 mm)	Gill net	1	1.31E-05		740
Fishing rod	4 anglers, \approx 60 h	$\frac{1}{2}$	0.05		14496
<i>Rhamdia quelen</i>					
Longline	3 longlines with 10 fish hooks	40	0.000889		14106
Gill net (20 m)	Gill net	31	0.000405		8133
Gill net (40 mm)	Gill net	33	0.000431		14768
Fishing rod	4 anglers, \approx 60 h	8	0.033333		1978

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